



## Spatial mapping of vulnerability hotspots: Information for mitigating vessel-strike risks to sea turtles

Ryan C. Welsh<sup>\*,1</sup>, Blair E. Witherington<sup>2</sup>

*Inwater Research Group, 4160 NE Hyline Dr., Jensen Beach, FL 34957, USA*

### ARTICLE INFO

#### Keywords:

Density surface model  
Distance sampling  
Transects  
Vessel strike  
Nesting beach  
Slow zone

### ABSTRACT

Mortality risk to imperiled animal populations from anthropogenic hazards can be managed by spatial limits on human behavior if exposure and vulnerability of the animals are known. To provide this information for sea turtles in waters near their nesting beaches, we mapped exposure to vessel strikes, which are a major, lethal hazard to these endangered animals. During the 2021 and 2022 nesting seasons, we carried out standardized transect line surveys off Florida's Atlantic coast, focusing on Loggerhead and Green Sea Turtles. Using Distance Sampling and Density Surface Modeling, we estimated the distribution of turtles near the surface (thus vulnerable to vessel strikes) based on several covariates. Our results revealed a clustering of vulnerable turtles near the shore and within hotspots identified by adjacent nesting beach density over tens of kilometers. Contrary to risk assessments based on stranding data, our findings present a new perspective on potential strike risk. We propose that our methodology and data can significantly contribute to initiating human behavioral changes required to reduce widespread vessel strikes on sea turtles.

### 1. Introduction

Coastal zones represent crucial intersections between vulnerable marine wildlife and anthropogenic hazards, including vessel strikes (Smallwood et al., 2012). To manage risks posed by these hazards, conservation measures are commonly applied selectively to Marine Protected Areas defined by spatial and temporal boundaries (Silber et al., 2012; Calleson and Frohlich, 2007). Ideally, these areas are justified by spatiotemporal information that can guide effective management of risk given practical consequences of that protection (Maxwell et al., 2014; Brander et al., 2020).

Vessel strikes are known to cause mortality in at least 75 species of marine vertebrates, including many threatened with extinction (Schoeman et al., 2020; <http://www.redlist.org>). Vessel strike mortality poses a significant threat to sea turtles and other marine animals, leading to population-level effects that can influence species recovery or decline (Chaloupka et al., 2008; Schoeman et al., 2020). These strikes leave conspicuous evidence in stranded sea turtles, presenting as crushing fractures and lacerations that often penetrate the carapace and compromise the coelomic cavity, leading to catastrophic injury or death (Work et al., 2010).

Evidence of vessel strikes causing death in sea turtles is widespread, with documented occurrences in various regions including the Galapagos Islands (Denkinger et al., 2013), Hawaiian Archipelago (Chaloupka et al., 2008), Queensland, Australia (Hazel and Gyuris,

\* Correspondence to: Inwater Research Group, 4160 NE Hyline Dr., Jensen Beach, FL, USA.

E-mail address: [rwelsh@inwater.org](mailto:rwelsh@inwater.org) (R.C. Welsh).

<sup>1</sup> ORCID ID: 0000-0002-4092-1328.

<sup>2</sup> ORCID ID: 0000-0002-3039-2151.

<https://doi.org/10.1016/j.gecco.2023.e02592>

Received 1 June 2023; Received in revised form 25 July 2023; Accepted 31 July 2023

Available online 1 August 2023

2351-9894/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

2006), Malaysia (Phu and Palaniappan, 2019), Mediterranean Sea (Casale et al., 2010), Canary Islands, Spain (Orós et al., 2005), Bermuda (Davenport and Davenport, 2006), and throughout the warmer waters of the southeastern and mid-Atlantic United States. (Ataman et al., 2021). In Florida, where sea turtle strandings are the highest in the U.S., vessel-strike evidence provides the most frequent, identifiable cause of sea turtle death (Foley et al., 2019).

Vessel strike evidence in strandings most occurs most often near inlets and channels associated with ports (Davenport and Davenport, 2006; Denkinger et al., 2013; Foley et al., 2019). This localized risk of strikes is presumably a function of the local hazard (vessel traffic density, speed, operator behavior) and exposure of turtles (localized numerical density and vulnerability). Florida serves as an example where high vessel-traffic locations (high-hazard areas) overlap with areas of high sea turtle abundance (high vulnerability areas), such as waters adjacent to nesting beaches during the spring and summer nesting season.

The vulnerability of adult turtles arises due to increased exposure as they mate or rest near the water's surface. Considering that high-density nesting beaches tend to aggregate these vulnerable turtles in larger numbers compared to surrounding waters, areas near these beaches become hotspots for potential vessel strikes. Consequently, boaters navigating these waters may face a heightened risk of inadvertently striking a turtle.

Foley et al. (2019) found that in Florida, vessel-strike injuries are most frequent in the adult life stage and in species that regularly nest on Florida beaches, such as loggerhead sea turtles (*Caretta caretta*), green sea turtles (*Chelonia mydas*), and leatherback sea turtles (*Dermodochelys coriacea*), which we will hereafter refer to as loggerhead, green turtle, and leatherback, respectively. Reproductively active males and females are also particularly well represented in these strandings (Foley et al., 2019). The high-density nesting beaches of southeastern Florida have received 66 % of the state's annually reported strandings with vessel-strike injuries (Foley et al., 2019), which over-represents the region's 17% of coastline. Annual counts of these injuries are increasing, with estimates of affected turtles numbering thousands per year (Foley et al., 2019).

During the breeding season, waters adjacent to nesting beaches contain sea turtles that are mating or resting during their inter-nesting period. These adult turtles are of high reproductive value to their populations (Crouse et al., 1987) and are commonly injured (Ataman et al., 2021) or killed (Foley et al., 2019) by vessel strikes. Sea turtles aggregate near Florida nesting beaches during spring and summer months (Witherington et al., 2009) and often linger near the surface as individuals or mating pairs (Fig. 1). Florida's leatherbacks begin nesting in late February with peak nesting in May, loggerheads begin nesting in April with a peak in June and July, and green turtles start nesting in late May with a peak between mid-June and mid-August (Florida Fish and Wildlife Conservation Commission - Fish and Wildlife Research Institute (FWC-FWRI), 2022). These nesting seasons are preceded by a breeding period during which mating occurs, partly near nesting beaches. The distribution of both inter-nesting females and mating pairs near the surface makes these turtles especially vulnerable to vessel strikes (Sobin and Tucker, 2008).

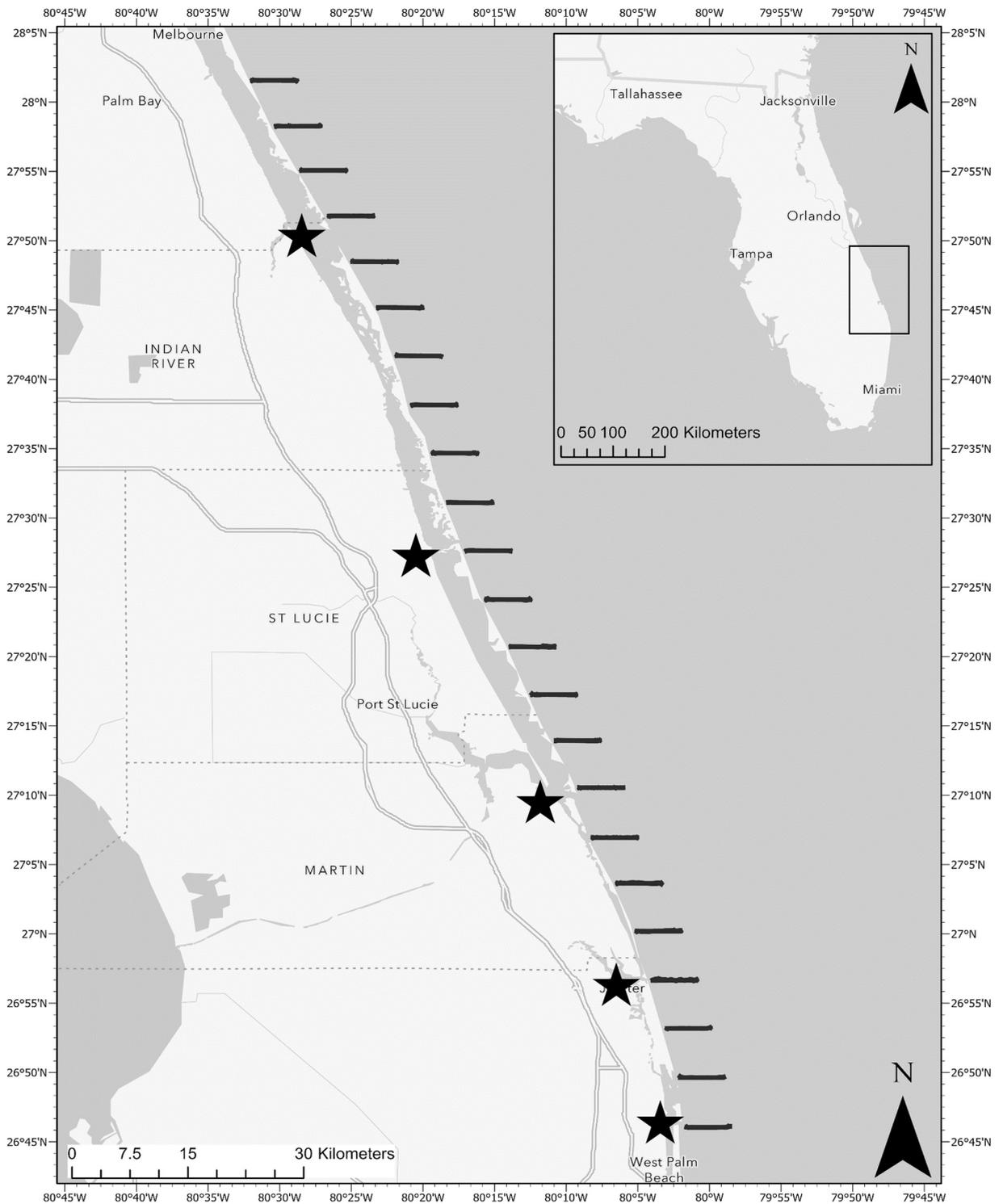
From Foley et al. (2019), we identified southeastern Florida as a location where distributions of vulnerable, nearshore, breeding sea turtles intersect with vessel hazards. In 2020 and 2021, the five southeastern Florida coastal counties represented by our sampling area (Brevard, Indian River, St. Lucie, Martin, Palm Beach) hosted more than 74 % of loggerhead, green turtle, and leatherback sea turtle nesting in the continental U.S. (Florida Fish and Wildlife Conservation Commission - Fish and Wildlife Research Institute (FWC-FWRI), 2022). In the same waters during this period, over 60,000 commercial and pleasure crafts were registered (Florida Highway Safety and Motor Vehicles (FLHSMV), 2022).

To reduce the threat of vessel strikes to sea turtles in Florida, recommendations from a recent workshop on reducing sea turtle



Fig. 1. Species recorded by this study—mating green turtle pair (above) and adult female loggerhead sea turtle (below).

vessel strikes in Florida (Fuentes et al., 2021) outlined the need for information that would guide management action. Social research from Fuentes et al. (2021) found that surveyed members of the boating public responded that they would support conservation intervention, such as speed zones, if they are supported by compelling evidence of their effectiveness. To generate this evidence, we



**Fig. 2.** Map of the surveyed Atlantic coast of Florida, featuring 23 standardized transect lines (black) and five inlets (stars, from north to south: Sebastian, Ft. Pierce, St. Lucie, Jupiter, and West Palm). Map modified from sources: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and GIS community.

conducted vessel-based surveys across a set of standardized transects to map the distribution of turtles within one meter of the surface who are at risk of vessel strikes. We defined these turtles as “vulnerable turtles” because they are within the typical “strike zone” or depth of water that an engine, propeller, skeg, or hull of a vessel sits at when underway, a measurement consistent with other vessel strike studies (Sobin and Tucker, 2008). Through these surveys, we aimed to 1) create a distribution map of vulnerable turtles across a densely occupied nearshore area off Florida’s most important nesting beaches and 2) identify spatial variables that might infer nearshore turtle distributions in other regions without transect line surveys. The resulting data can guide management action to reduce the threat of vessel strikes to sea turtles in Florida and beyond.

## 2. Methods

### 2.1. Study area

Our study area was located on the Atlantic coast of Florida, USA (Fig. 2). We established 23 transect lines between Palm Beach Inlet (N26.76726, W80.02632) and the northern border of the Archie Carr National Wildlife Refuge (N28.02613, W80.53159), covering an approximately 150-kilometer stretch of coastline. These transects spanned five inlets along the Florida coast (Palm Beach Inlet, Jupiter Inlet, St. Lucie Inlet, Ft. Pierce Inlet, and Sebastian Inlet) allowing access for mariners to nearshore waters. The study region contains the highest densities of adult loggerhead and green sea turtle strandings with vessel strike injuries in the state (Foley et al., 2019). This area also has nearshore hard-bottom reef systems known to be extensively used by juvenile green turtles (Ehrhart et al., 1996).

### 2.2. Transect surveys

Each of the 23 parallel transects we designed was oriented east-west along an approximately north-south coastline. These transects were each five kilometers long with a landward boundary approximately 500 m from shore, a distance from the shore ensuring safe operation of the survey vessel away from breaking waves. The parallel transect lines were separated by 6.75 kilometers to minimize the likelihood of turtles moving between transects, while also ensuring a low standard error in the spatial modelling between adjacent transects. The transects required two days to survey at a vessel speed of approximately 12 km/hr. We conducted surveys during four periods in May and June of 2021 and 2022. These months were chosen because they coincided with the arrival of nesting loggerhead and green turtles, as well as the peak of mating for green turtles off these nesting beaches. During each four-day sampling period, we surveyed the transects, then re-surveyed them in reverse order. This survey design aimed to account for potential temporal variations/correlations (time of day, month of year, and differing years) and the stochasticity of environmental factors (environmental variables collected during surveys; Table 1.) of both sighting conditions and turtle presence/absence.

We conducted line transect surveys as described in Welsh and Mansfield (2022), with two observers atop an elevated platform (eye-level = 4.5 m above sea level) on an 8.2 m survey vessel. While underway, a helmsman ensured the survey vessel stayed on course and recorded turtle locations with a Garmin Global Positioning System unit. A separate individual recorded data in real time from the observers. Environmental data were recorded prior to the start of each transect (Table 1). For each turtle observation, we recorded species, size class, position in the water column, and perpendicular distance from the transect line (Table 1).

### 2.3. Analysis

Because our analysis aimed to determine the distribution of Turtles Vulnerable to Vessel Strikes, we only included turtles observed within one meter of the water’s surface in the analysis. We performed distance sampling analysis using Mark Recapture Distance

**Table 1**

Environmental condition data recorded during study. Included are definitions of each covariate and when the data were collected during transects.

Data recorded	Method of data collection
Beaufort State	Measured using the Beaufort Scale, combining both wind speed and wave heights, recorded at the start of each transect
Cloud Cover	Measured categorically in 25 % increments. 1 = ≤ 25 %, 2 = 26–50 %, 3 = 51–75 %, 4 ≥ 76 %, recorded at start of each transect
Distance	Perpendicular distance (m) of an observed turtle from the transect line, as visually estimated by the original observer
Life Stage	“Adult,” “Sub-adult,” and “Juvenile” life stages determined by the observer using the relative size of the carapace (observers had experience with hundreds of these determinations verified by capture and measurement)
Location	GPS waypoint representing the sighting of turtles along the transect line
Location in Water Column	Turtle’s depth in the water column at the moment of observation. Measured categorically as At Surface, Within 1 m of the surface, and deeper than 1 m
Mating Pair	Turtles sighted as a mating pair
Month	Measured categorically as a number indicating the month surveys took place
Species	Species of observed animal
Water Clarity	Observer consensus of the maximum depth of observable objects through the water column, recorded at the start of each transect. A minimum of 1 m of clarity was needed to ensure all observations on the transect line could be made
Water Temperature	Taken from the vessel’s transponder, measured in Celsius, and recorded at the start of each transect
Wave Height	Measured in feet and placed categorically in 4 increments. 0, 1–2, 2–3, and 3–4, recorded at the start of each transect
Wind Speed	Measured in miles per hour by an anemometer, recorded at the start of each transect
Year	Year observation was made

sampling in program R using the package *Distance* (Miller et al., 2019a). Distance data were binned to account for rounding errors in observations. We considered both hazard rate and half-normal decay functions as candidate detection functions. Sightings were truncated where the detection probability fell to under 0.15 as per Buckland et al. (2004). We ran 14 models for each candidate function: one with no covariates and 13 with each of the temporal and environmental covariates observed (Table 1). Model selection among the set of candidate models was done using Akaike information criteria (AIC, Akaike, 1998). We considered models with  $\Delta$ AIC values less than two commensurate, with the final model selection based on principles of parsimony, visual examination of the probability detection curve and a  $\chi^2$  goodness of fit test ( $\alpha = 0.05$ ), provided in the package *Distance* (Miller et al., 2019a).

To map distribution with spatially inclusive covariates, we used Density Surface Modeling (DSM, Thomas et al., 2010) within the R package *DSM* (Miller et al., 2019b). We divided the entirety of the field area into 200 m<sup>2</sup> sections, which is equal to roughly twice the truncation length of our best fit detection function as recommended by Buckland et al. (2004). We implemented generalized additive models using a logarithmic link and a negative binomial error distribution. This error distribution choice served to address potential overdispersion and zero-inflation issues inherent to the segmented nature of our transects. We used extra shrinkage terms on each smoothing and incorporated the selected detection function to generate estimated abundance values for each 200 m<sup>2</sup> segment. We tested five different spatial covariates: bathymetry, distance from shore, distance from inlet, annual nesting density of adjacent beaches, and latitude/longitude (spatial extent). Bathymetry data were collected from NOAA (<https://www.ngdc.noaa.gov/mgg/coastal/grddas03/grddas03.htm>). Data for nesting density of adjacent sea turtle nesting beaches came from the Florida Fish and Wildlife Conservation Commission Statewide Nesting Beach Survey (SNBS) (Brost et al., 2015).

We used the five-year average (2017–2021) of green turtle and loggerhead sea turtle nest density (nests/km shoreline) recorded by the SNBS over the entirety of the nesting beaches directly adjacent to our field site. Although data from 2022 were not available during this analysis, these annual counts are known to be strongly spatially consistent between years (Witherington et al., 2009). Based on tracking studies (Hart et al., 2010; Sloan et al., 2022), inter-nesting turtles often stray from waters directly offshore from where they nested. To account for this spatial lag effect, we evaluated the 5-year nesting density at varying spatial scales, each represented by 'blocks' of area that were 1, 5, 10, 15, 20, 25, or 30 km in length on each side. This was achieved by first adjusting the average nest densities of each SNBS beach (range 0.3–21.0 km) to a per-kilometer resolution. In sections where a kilometer encompassed multiple SNBS beach segments, we proportionally allocated the average nest density based on the respective lengths of the beach segments within the kilometer. This approach allowed us to maintain a consistent spatial resolution across our study area. The per-kilometer nest densities allowed us to re-scale nesting beach density blocks as needed. We also assigned nesting beach densities to a block representing a larger geographic scope, defined as the span between ocean inlets (37–63 km). These varying resolutions were tested alongside other spatial covariates.

We tested for multicollinearity of spatial covariates using a Pearson's correlation coefficient. DSM models were run using each spatial covariate, as well as all additive covariate combinations. Candidate models with  $\Delta$ AIC values less than two were considered commensurate, with model selection based on the principles of parsimony. Using the selected model, we derived abundances for areas that were not directly surveyed using model inference through the package *DSM* (Miller et al., 2019b). This package worked in conjunction with ESRI's ArcGIS to create prediction grids of estimated abundance for the entire field area.

### 3. Results

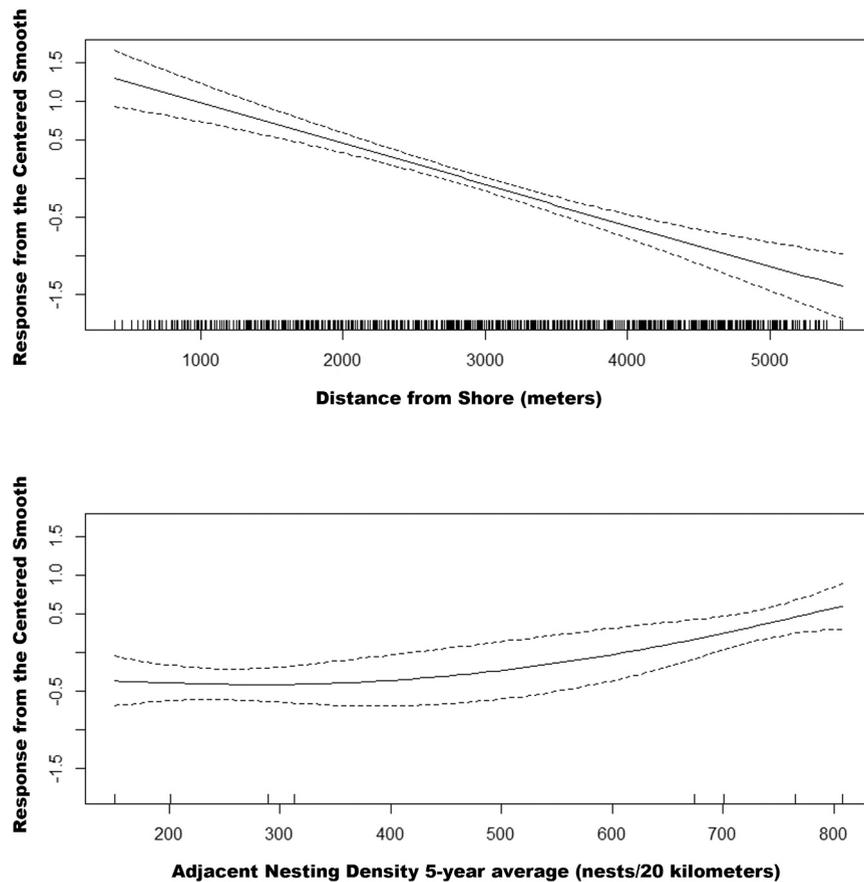
Over the two-year sampling period, we conducted surveys covering 460 km, which represented an area of approximately 887 km<sup>2</sup>. We observed 354 turtles that were within one meter of the surface and considered vulnerable to vessel strikes at the time of sighting. This included 171 loggerheads, 181 green turtles, and 2 leatherbacks. Specifically, the loggerhead observations comprised 71 adults and 22 sub-adults. The green turtles observed included 167 adults and 14 juveniles. The leatherbacks comprised 2 adults.

The best fit detection function for vulnerable turtles was a half-normal curve with the covariate, "Location in Water Column" (Table 1, Fig. S1). There were two candidate models for best fit DSM of vulnerable turtles, but the additive model of spatial extent, Distance to Shore, and 20-km average Adjacent Nesting Beach Density (Table 2, Fig. 3) was chosen due to parsimony. The best-fit DSM provided an estimate of 5717 (95 % CI 4490–7280) turtles within one meter of the surface, and thus vulnerable to vessel strikes, at any given time over the two-year study period across the entirety of the study area. This figure is not a count of individual turtles but an estimate of the number of turtles at risk from vessel strikes at any point in time during our study. The DSM-produced density-distribution heatmaps demonstrated the influence that spatial covariates had on the model (Figs. 3 & 4). A distinct linear relationship was evident between Distance to Shore and the number of Turtles Vulnerable to Vessel Strike, with the number increasing as Distance to Shore decreased (Fig. 3). Approximately 80 % of all modeled Turtles Vulnerable to Vessel Strike were estimated to occur within

**Table 2**

Commensurate best fit density surface models with lowest AIC scores for the spatial covariates: Spatial Extent, Adjacent Nesting Beach Average, Water Depth, and Distance from Shore, for Turtles Vulnerable to Vessel Strikes observed off Florida's Atlantic coast. The model in bold was the selected model based on the principles of parsimony.

Covariates	AIC score	REML	Deviance explained (%)
<b>Spatial Extent + Distance from Shore (m) + Adjacent Nesting Beach Average (20 km)</b>	<b>3068.50</b>	<b>1538.61</b>	<b>11.99</b>
Spatial Extent + Water Depth (m) + Distance from Inlet (m) + Adjacent Nesting Beach Average (20 km) + Distance from Shore (m)	3068.26	1538.27	12.19



**Fig. 3.** Plots of covariate effects on selected Density Surface Model (additive model of Spatial Extent, Distance from Shore, and Adjacent Nesting Beach Average). Response from the centered smooth (y-axis) represents the response of the model to both Distance from Shore and Adjacent Nesting Density. The dotted lines represent the 95 % CI of the model. Hash marks on the x-axis represent data points used for each covariate.

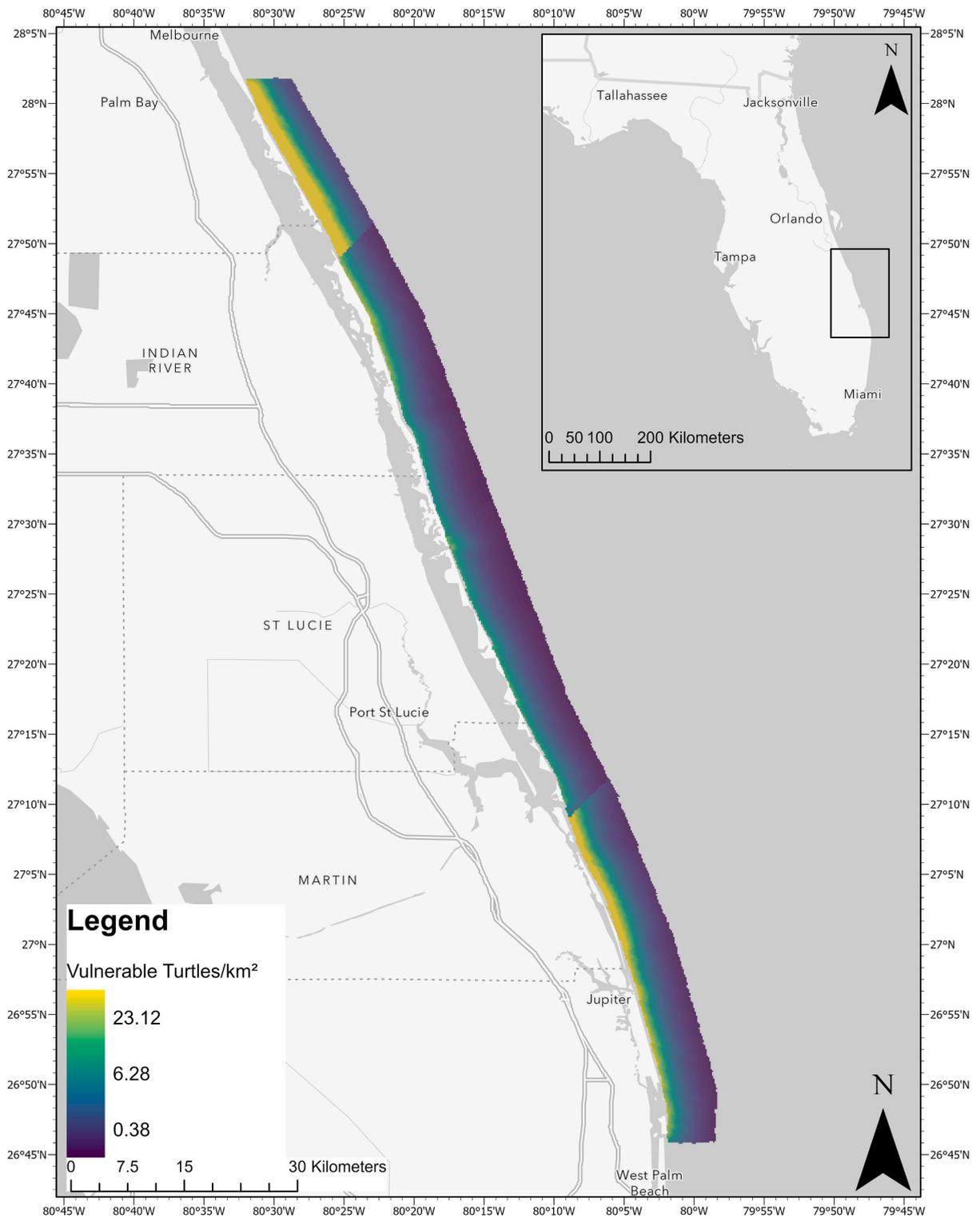
3000 m of shore. Adjacent Nesting Beach Density (Fig. 3) also highlighted at least two high-density areas, as evidenced by the sharp and immediate rises in density shown in Fig. 4. These abrupt changes correspond with similar increases in nesting beach density, predominantly associated with the Archie Carr National Wildlife Refuge in the study area's northern region, and the beaches of Tequesta, Jupiter, and Juno Beach in the southern region.

## 4. Discussion

### 4.1. Applied abundance measurements

Density Surface Models are an important and emerging tool for understanding sea turtle spatial distributions (Archibald and James, 2016; DiMatteo et al., 2022; Welsh and Mansfield, 2022). Although these models have been used elsewhere to describe vessel-strike hotspots for cetacean species in Australia (Mayaud et al., 2022), Canada (Wright et al., 2021), and France and Italy (Grossi et al., 2021), they have yet to be used to show susceptibility of sea turtles to this threat. We show that these versatile models are uniquely suited to describe coastal exposure of sea turtles to vessel strike hazards, in a way that is easily interpreted by resource managers. Our analysis showed that a vessel management zone closest to shore would be most effective in protecting mating and inter-nesting period sea turtles from vessel strikes off Florida nesting beaches. The analysis also showed that these protections would be effective if limited further to specific, regional hotspots. The hotspots for sea turtle vulnerability that we discovered are associated with the densely nested beaches of southern Brevard County (Archie Carr National Wildlife Refuge) and the beaches of southern Martin and northern Palm Beach counties (Fig. 4, Table S1).

The uneven spatial distribution we measured was driven by positive correlations between the spatial density of vulnerable turtles and two key factors — 1) proximity to shore, and 2) spatial nest density on adjacent beaches at a resolution of 20 km blocks. These factors drove estimates of vulnerable, near-surface turtles during the breeding season, which were the focus of our study. Describing spatial distributions of other turtle subsets would require attention to turtle availability for observation and an additional representative sampling of seasons, habitats, and sea conditions. Broader surveys seem likely to reveal additional spatiotemporal



**Fig. 4.** Density distribution map created from the best fit Density Surface Model (additive model of Spatial Extent, Distance from Shore, and Adjacent Nesting Beach Average) for vulnerable turtles off the eastern coast of Florida (USA) 2021–2022.

(a) The map is modified from Map sources: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community.

concentrations of vulnerable sea turtles. For example, extensive surface-basking by loggerhead sea turtles of varied sizes over rocky hardbottom habitats off the southeastern United States is common (Frick et al., 2000). We also expect these animals to have a high vulnerability to vessel strikes.

Although it may seem intuitive that sea turtle nesting density would determine the adjacent, in-water abundance and distribution of adult turtles during the breeding season, this assumption had not been tested prior to the present study. We showed that beaches with the highest densities of nesting turtles are associated with the highest abundance of turtles within 1 m of the water's surface, and thus, most vulnerable to vessel strikes. It is important to note that our study did not investigate the abundance of turtles in deeper waters, and our conclusions are limited to the area within 1 m of the surface. Nonetheless, our findings justify the spatial boundaries for a coastal safety zone that would protect sea turtles from vessel strikes. We acknowledge the need for further research to fully understand the complex spatiotemporal distributions of breeding sea turtles near their nesting beaches.

Beyond application to threats management, spatial mapping from DSM provides information with which to represent marine regions with standardized line transects to assess temporal trends. For this purpose, a short time series of detailed DSM would guide the representation of less spatially extensive transects surveyed over a longer time series.

#### 4.2. Contribution of spatial data to speed and vigilance zones

Vessel speed zones are an alternative to vessel exclusion zones where animals need protection from vessel strikes but where exclusion would be unacceptable to mariners. Marine animals shown to benefit from vessel speed zones include the North Atlantic right whale (*Eubalaena glacialis*, Rockwood et al., 2020) and the Florida manatee (*Trichechus manatus latirostris*, Udell et al., 2019). Reduced speed is reasoned to reduce vessel strike risk by lengthening reaction time for the vessel operator and for the vulnerable animal, and by reducing the severity of injuries in the event of a strike (Calleson and Frohlich, 2007; Work et al., 2010).

Vessel speed zones are easily considered to be narrowly applied Marine Protected Areas (Bakker, 2022). All are areas where human behavior is managed to protect marine wildlife or ecosystems. There is extensive literature on effectiveness of marine protected areas as a function of location, size, contained resources, and regulatory measures (reviewed by Pendleton et al., 2018). Consideration of all these factors within a cost-benefit analysis is reasoned to be critical for human behavior change in terms of acceptance and compliance (Maxwell et al., 2014; Brander et al., 2020).

We propose that although spatiotemporal information on density of vulnerable turtles is a key element to guide placement of sea turtle protection zones, additional data would inform a cost-benefit analysis of where and when these zones would be most successful. Speed zones affect boater access, which has socioeconomic costs expressed as resistance to successful implementation (Jett et al., 2009). Even voluntary speed reduction zones or enhanced vigilance zones have costs that apply to effectiveness, given that inconvenience and vigilance effort weigh against compliance. In a study of boater perceptions of what behavior change they might accept at a known hotspot for vessel strikes, Fuentes et al. (2021) found that only half of responding boaters would be likely to promote practices to reduce harm to wildlife.

In an analysis of vessel-speed zones to protect Florida manatees (*Trichechus manatus latirostris*), Udell et al. (2019) modelled vessel-strike risk, and cost reflected by regulatory burden on boaters, to present a spatiotemporal and qualitative spectrum of zones that would either minimize risk to manatees or minimize cost of implementation. Implementation of sea turtle zones would greatly benefit from a similar analysis. A default regulatory decision might be to minimize risk at the expense of socioeconomic cost. In their examination of sea turtle vessel-strike mortality in Florida, Foley et al. (2019) found that areas with high boating traffic, namely, inlets, navigation channels, and marinas, showed the highest number of vessel strikes among all sea turtle life stages, and that the location and timing of most adults stranding with vessel strikes corresponded with major nesting beaches fronting open waters. Foley et al. recommended that each of these areas be protected but presented only assumptions about comparative densities of vulnerable turtles. We agree that both high-traffic waters and waters off nesting beaches require protection but recognize that characteristics of these locations vary in ways that affect potential success of protection zones.

In the absence of a complete cost-benefit analysis for sea turtle protection zones, we argue that spatiotemporal information on density of vulnerable turtles should guide zone placement. This argument relies on reasonable assumptions about expected socioeconomic costs. Among competing locations for sea turtle protection, either by go-slow or enhanced vigilance zones, units in cost-benefit analyses would include size of the proposed zone, number of vulnerable turtles contained, number of boaters affected, and magnitude of this effect per boater. An open water area off a nesting beach may require a larger zone area than an inlet or channel, but the nesting zone is likely to encompass more turtles per area and affect far fewer boaters. Another way to consider cost and benefit is from the perspective of an individual boater. To a boater, one might assume that slow travel is considered a cost and that avoiding turtle strikes is a benefit. Regardless of how many turtles are struck by fellow boaters in a given area, the individual's risk is solely dependent upon their vessel speed and density of vulnerable turtles at the boater's location. Thus, a boater might logically decide to reduce speed where turtles are frequent and increase speed where they are less so.

We encourage additional estimations of vessel-strike vulnerable turtles in areas shown to be hotspots for vessel strikes. Our own work off nesting beaches has shown that waters closest to the beach, and off the highest density nesting areas, would be effective locations for protection zones. We propose that focusing reduction of vessel-strike hazards where sea turtle vulnerability is highest minimizes societal cost of hazard-reduction compliance (fewer zones and times requiring fewer mariners to change behavior) and is more likely to gain acceptance.

### 4.3. Conclusions and policy implications

Our analysis identified areas closest to shore and adjacent to the most densely nested beaches as hotspots for vulnerable sea turtle density. We also showed that nest-count density nearby, at a scale of tens of kilometers, was a good predictor of the number of Turtles Vulnerable to Vessel Strikes. This effort provides the first guidance for designation of zones to protect sea turtles from vessel strikes based on an empirical distribution of vulnerable sea turtles.

We argue that the vulnerability hotspots we revealed are a more reliable and unbiased indicator of potential vessel-strike risk than the frequency and location of strandings with vessel-strike evidence. In addition to incomplete reporting of strandings (Nero et al., 2013), strandings reveal the result of strikes rather than the potential for them. Localized risk of strikes is a function of vessel hazards (traffic density, speed, operator behavior) and exposure of turtles (localized numerical density and vulnerability). We propose that an effective policy would be to reduce hazard potential where turtles are most vulnerable, which might not correspond to where vessel traffic is highest and where strandings are most frequent. Risk reduction by vessel operators (minimizing the probability of striking a turtle) might include location-specific enhanced vigilance and slower speed. Risk reduction for sea turtles in the nearshore zone may also benefit the reduction of human injury. During our study, we observed ocean swimmers, stand-up paddle boarders, kayaks, small fishing vessels, surfers, and kite surfers in this zone.

There is evidence that spatial information on sea turtle distributions can reduce vessel-strike mortality by using the data to shape vessel speed zones and boating behavior, either voluntarily or mandated (Work et al., 2010; Shimada et al., 2017). Go-slow zones in Moreton Bay, Australia protected loggerhead and green sea turtles to the extent that these zones overlapped with habitat use, especially in shallow waters (Shimada et al., 2017). We propose that vessel-strike protection zones targeted using detailed data might avoid the “cry-wolf effect.” This effect describes human behavioral responses to warnings, and it applies to voluntary action urged within the framework of zoning (LeClerc and Joslyn, 2015). When regulatory zoning is nonspecific, compliance is low (Papastavrou and Lehto, 1996). We suggest that our data products describe specific and discrete sea turtle protection (awareness, vigilance, safety) zones that would be effective from the perspectives of promulgation, implementation, and compliance (Fuentes et al., 2021).

### CRedit authorship contribution statement

**Ryan C Welsh:** Formal analysis, Data curation, Writing – original draft, Methodology, Investigation, Visualization, Funding acquisition, Conceptualization, Supervision. **Blair E. Witherington:** Conceptualization, Methodology, Supervision, Investigation, Writing – original draft, Funding acquisition, Visualization.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data Availability

Data will be made available on request.

### Acknowledgements

The authors would like to thank R. Chabot, D. Witherington, R. Newman, M. Bresette, A. Garstin, D. Clark, S. Weege, S. Traxler, and the staff and volunteers at The Nature Conservancy-Blowing Rocks Preserve for their assistance in study design and fieldwork. Thank you to J. Guertin, A. Michaels and A. Fisher for providing edits. This study was funded by Inwater Research Group and the Sea Turtle License Plate Grants Program, Grants 20-011R and 22-009R.

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02592](https://doi.org/10.1016/j.gecco.2023.e02592).

### References

- Akaike, H., 1998. Information theory and an extension of the maximum likelihood principle. In: Parzen, E., Tanabe, K., Kitagawa, G. (Eds.), Selected Papers of Hirotugu Akaike. Springer, New York, pp. 199–213. [https://doi.org/10.1007/978-1-4612-1694-0\\_15](https://doi.org/10.1007/978-1-4612-1694-0_15).
- Archibald, D.W., James, M.C., 2016. Evaluating inter-annual relative abundance of leatherback sea turtles in Atlantic Canada. *Mar. Ecol. Prog. Ser.* 547, 233–246. <https://doi.org/10.3354/meps11648>.
- Ataman, A., Gainsbury, A.M., Manire, C.A., Hoffmann, S.L., Page-Karjian, A., Hirsch, S.E., Klingshirn, S., et al., 2021. Evaluating prevalence of external injuries on nesting loggerhead sea turtles *Caretta caretta* in southeastern Florida, USA. *Endanger. Species Res.* 46, 137–146. <https://doi.org/10.3354/esr01149>.
- Bakker, K., 2022. Smart oceans: artificial intelligence and marine protected area governance. *Earth Syst. Gov.* 13, 100141 <https://doi.org/10.1016/j.esg.2022.100141>.

- Brander, L.M., Van Beukering, P., Nijsten, L., McVittie, A., Baulcomb, C., Eppink, F.V., van der Lelij, J.A.C., 2020. The global costs and benefits of expanding Marine Protected Areas. *Mar. Policy* 116, 103953. <https://doi.org/10.1016/j.marpol.2020.103953>.
- Brost, B., Witherington, B., Meylan, A., Leone, E., Ehrhart, L., Bagley, D., 2015. Sea turtle hatchling production from Florida (USA) beaches, 2002–2012, with recommendations for analyzing hatching success. *Endanger. Species Res.* 27 (1), 53–68. <https://doi.org/10.3354/esr00653>.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2004. *Advanced Distance Sampling*, 2. Oxford University Press, Oxford.
- Calleson, C.S., Frohlich, R.K., 2007. Slower boat speeds reduce risks to manatees. *Endanger. Species Res.* 3, 295–304. <https://doi.org/10.3354/esr00056>.
- Casale, P., Affronte, M., Insacco, G., Freggi, D., Vallini, C., Pino d'Astore, P., Argano, R., et al., 2010. Sea turtle strandings reveal high anthropogenic mortality in Italian waters. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 20 (6), 611–620. <https://doi.org/10.1002/aqc.1133>.
- Chaloupka, M., Work, T.M., Balazs, G.H., Murakawa, S.K., Morris, R., 2008. Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian Archipelago (1982–2003). *Mar. Biol.* 154 (5), 887–898. <https://doi.org/10.1007/s00227-008-0981-4>.
- Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68 (5), 1412–1423. <https://doi.org/10.2307/1939225>.
- Davenport, J., Davenport, J.L., 2006. The impact of tourism and personal leisure transport on coastal environments: a review. *Estuar. Coast. Shelf Sci.* 67, 280–292. <https://doi.org/10.1016/j.ecss.2005.11.026>.
- Denkinger, J., Parra, M., Muñoz, J.P., Carrasco, C., Murillo, J.C., Espinosa, E., Koch, V., et al., 2013. Are boat strikes a threat to sea turtles in the Galapagos Marine Reserve? *Ocean Coast. Manag.* 80, 29–35. <https://doi.org/10.1016/j.ocecoaman.2013.03.005>.
- DiMatteo, A., Canadas, A., Roberts, J., Sparks, L., Panigada, S., Boisseau, O., Moscrop, A., Fortuna, C.M., Lauriano, G., Holcer, D., Peltier, H., 2022. Basin-wide estimates of loggerhead turtle abundance in the Mediterranean Sea derived from line transect surveys. *Front. Mar. Sci.* 9 <https://doi.org/10.3389/fmars.2022.930412>.
- Ehrhart, L.M., Redfoot, W.E., Bagley, D.A., 1996. *A Study of the Population Ecology of In-water Marine Turtle Populations on the East-central Florida Coast from 1982 to 96*. Comprehensive Final Report to US Dept. of Commerce-NOAA, National Marine Fisheries Service, Miami, Florida, USA.
- Florida Fish and Wildlife Conservation Commission - Fish and Wildlife Research Institute (FWC-FWRI), 2022. *Statewide Nesting Beach Survey program database as of 1 October 2022*.
- Florida Highway Safety and Motor Vehicles (FLHSMV), 2022. (<https://www.flhsmv.gov/pdf/vessels/vesselstats2021.pdf>).
- Foley, A.M., Stacy, B.A., Hardy, R.F., Shea, C.P., Minch, K.E., Schroeder, B.A., 2019. Characterizing watercraft-related mortality of sea turtles in Florida. *J. Wildl. Manag.* 83 (5), 1057–1072. <https://doi.org/10.1002/jwmg.21665>.
- Frick, M.G., Slay, C.K., Quinn, C.A., Windham-Reid, A., Duley, P.A., Ryder, C.M., Morse, L.J., 2000. Aerial observations of courtship behavior in loggerhead sea turtles (*Caretta caretta*) from southeastern Georgia and northeastern Florida. *J. Herpetol.* 34 (1), 153–158. <https://doi.org/10.2307/1565255>.
- Fuentes, M.M., Meletis, Z.A., Wildermann, N.E., Ware, M., 2021. Conservation interventions to reduce vessel strikes on sea turtles: a case study in Florida. *Mar. Policy* 128, 104471. <https://doi.org/10.1016/j.marpol.2021.104471>.
- Grossi, F., Lahaye, E., Moulins, A., Borroni, A., Rosso, M., Tepsich, P., 2021. Locating ship strike risk hotspots for fin whale (*Balaenoptera physalus*) and sperm whale (*Physeter macrocephalus*) along main shipping lanes in the North-Western Mediterranean Sea. *Ocean Coast. Manag.* 212, 105820 <https://doi.org/10.1016/j.ocecoaman.2021.105820>.
- Hart, K.M., Zawada, D.G., Fujisaki, I., Lidz, B.H., 2010. Inter-nesting habitat-use patterns of loggerhead sea turtles: enhancing satellite tracking with benthic mapping. *Aquat. Biol.* 11 (1), 77–90. <https://doi.org/10.3354/ab00296>.
- Hazel, J., Gyuris, E., 2006. Vessel-related mortality of sea turtles in Queensland, Australia. *Wildl. Res.* 33 (2), 149–154. <https://doi.org/10.1071/WR04097>.
- Jett, J.S., Thapa, B., Ko, Y.J., 2009. Recreation specialization and boater speed compliance in manatee zones. *Hum. Dimens. Wildl.* 14 (4), 278–292. <https://doi.org/10.1080/10871200902905984>.
- LeClerc, J., Joslyn, S., 2015. The cry wolf effect and weather-related decision making. *Risk Anal.* 35, 385–395. <https://doi.org/10.1111/risa.12336>.
- Maxwell, S.M., Ban, N.C., Morgan, L.E., 2014. Pragmatic approaches for effective management of pelagic marine protected areas. *Endanger. Species Res.* 26 (1), 59–74. <https://doi.org/10.3354/esr00617>.
- Mayaud, R., Castrillon, J., Wilson, C., Peel, D., Smith, J.N., Dalle Luche, G., Allen, J., Nash, S.B., 2022. Traffic in a nursery: ship strike risk from commercial vessels to migrating humpback whales (*Megaptera novaeangliae*) in a rapidly developing Australian urban embayment. *Mar. Policy* 146, 105332. <https://doi.org/10.1016/j.marpol.2022.105332>.
- Miller, D.L., Rextad, E., Burt, L., Bravington, M.V., Sedley, S., 2019b. dsm: density surface modelling of distance sampling data. (<https://cran.r-project.org/web/packages/dsm/dsm.pdf>). (Accessed 11 September 2022).
- Miller, D.L., Rextad, E., Thomas, L., Marshall, L., Laake, J.L., 2019a. Distance sampling in R. *J. Stat. Softw.* 89 (1), 1–28. <https://doi.org/10.18637/jss.v089.i01>.
- Nero, R.W., Cook, M., Coleman, A.T., Solangi, M., Hardy, R., 2013. Using an ocean model to predict likely drift tracks of sea turtle carcasses in the north central Gulf of Mexico. *Endanger. Species Res.* 21, 191–203. <https://doi.org/10.3354/esr00516>.
- Oros, J., Torrent, A., Calabuig, P., Déniz, S., 2005. Diseases and causes of mortality among sea turtles stranded in the Canary Islands, Spain (1998–2001). *Dis. Aquat. Org.* 63 (1), 13–24. <https://doi.org/10.3354/dao063013>.
- Papastavrou, J.D., Lehto, M.R., 1996. Improving the effectiveness of warnings by increasing the appropriateness of their information content: some hypotheses about human compliance. *Saf. Sci.* 21, 175–189. [https://doi.org/10.1016/0925-7535\(95\)00060-7](https://doi.org/10.1016/0925-7535(95)00060-7).
- Pendleton, L.H., Ahmadiya, G.N., Browman, H.I., Thurstan, R.H., Kaplan, D.M., Bartolino, V., 2018. Debating the effectiveness of marine protected areas. *ICES J. Mar. Sci.* 75 (3), 1156–1159. <https://doi.org/10.1093/icesjms/fsx154>.
- Phu, J.L., Palaniappan, P., 2019. Recaptured wild green turtles (*Chelonia mydas*) with newly documented boat strike injuries in Mabul Island, Sabah, Malaysia. *Chelonian Conserv. Biol.* 18 (2), 265–272. <https://doi.org/10.1016/j.ocecoaman.2017.03.028>.
- Rockwood, R.C., Adams, J., Silber, G., Jahncke, J., 2020. Estimating effectiveness of speed reduction measures for decreasing whale-strike mortality in a high-risk region. *Endanger. Species Res.* 43, 145–166. <https://doi.org/10.3354/esr01056>.
- Schoeman, R.P., Patterson-Abrolat, C., Plón, S., 2020. A global review of vessel collisions with marine animals. *Front. Mar. Sci.* 7, 292. <https://doi.org/10.3389/fmars.2020.00292>.
- Shimada, T., Limpus, C., Jones, R., Hamann, M., 2017. Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean Coast. Manag.* 142, 163–172. <https://doi.org/10.1016/j.ocecoaman.2017.03.028>.
- Silber, G.K., Vanderlaan, A.S., Arcercedillo, A.T., Johnson, L., Taggart, C.T., Brown, M.W., Bettridge, S., Sagarminaga, R., 2012. The role of the International Maritime Organization in reducing vessel threat to whales: process, options, action and effectiveness. *Mar. Policy* 36, 1221–1233.
- Sloan, K.A., Addison, D.S., Glinksky, A.T., Bencotter, A.M., Hart, K.M., 2022. Inter-nesting movements, migratory pathways, and resident foraging areas of green sea turtles (*Chelonia mydas*) satellite-tagged in Southwest Florida. *Front. Mar. Sci.* 1798. <https://doi.org/10.3389/fmars.2021.775367>.
- Smallwood, C.B., Beckley, L.E., Moore, S.A., 2012. Influence of zoning and habitats on the spatial distribution of recreational activities in a multiple-use marine park. *Coast. Manag.* 40, 381–400. <https://doi.org/10.1080/08920753.2012.692312>.
- Sobin, J.M., Tucker, T.D., 2008. Diving behavior of female loggerhead turtles (*Caretta caretta*) during their internesting interval and an evaluation of the risk of boat strikes. *OCEANS 2008*, 1–10. <https://doi.org/10.1109/OCEANS.2008.5152080>.
- Thomas, L., Buckland, S.T., Rextad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Burnham, K.P., et al., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47 (1), 5–14. <https://doi.org/10.1111/j.1365-2664.2009.01737.x>.
- Udell, B.J., Martin, J., Fletcher Jr, R.J., Bonneau, M., Edwards, H.H., Gowan, T.A., Hardy, S.K., Gurarie, E., Calleson, C.S., Deutsch, C.J., 2019. Integrating encounter theory with decision analysis to evaluate collision risk and determine optimal protection zones for wildlife. *J. Appl. Ecol.* 56 (5), 1050–1062. <https://doi.org/10.1111/1365-2664.13290>.
- Welsh, R.C., Mansfield, K.L., 2022. Intraspecific spatial segregation on a green turtle foraging ground in the Florida Keys, USA. *Mar. Biol.* 169 (2), 1–13. <https://doi.org/10.1007/s00227-021-04012-9>.

- Witherington, B., Kubilis, P., Brost, B., Meylan, A., 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. *Ecol. Appl.* 19 (1), 30–54. <https://doi.org/10.1890/08-0434.1>.
- Wright, B.M., Nichol, L.M., Doniol-Valcroze, T., 2021. Spatial density models of cetaceans in the Canadian Pacific estimated from 2018 ship-based surveys. *DFO Can. Sci. Advis. Sec. Res. Doc.* (2021/049. viii + 46 p).
- Work, P.A., Sapp, A.L., Scott, D.W., Dodd, M.G., 2010. Influence of small vessel operation and propulsion system on loggerhead sea turtle injuries. *J. Exp. Mar. Biol. Ecol.* 393 (1–2), 168–175. <https://doi.org/10.1016/j.jembe.2010.07.019>.